The reluctant innovator: orangutans and the phylogeny of creativity

van Schaik, C P ; Burkart, J M ; Damerius, Laura ; Forss, Sofia ; Koops, Kathelijne ; van Noordwijk, M A ; Schuppli, Caroline

DOI: https://doi.org/10.1098/rstb.2015.0183

Originally published at:
van Schaik, C P; Burkart, J M; Damerius, Laura; Forss, Sofia; Koops, Kathelijne; van Noordwijk, M A; Schuppli, Caroline (2016). The reluctant innovator: orangutans and the phylogeny of creativity. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 371(1690):20150183.
DOI: https://doi.org/10.1098/rstb.2015.0183

PHILOSOPHICAL
TRANSACTIONS B

The reluctant innovator: orang-utans and the phylogeny of creativity

Journal:	*Philosophical Transactions B*
Manuscript ID	RSTB-2015-0183.R2
Article Type:	Review
Date Submitted by the Author:	n/a
Complete List of Authors:	van Schaik, Carel; University of Zurich, Anthropological Institute & Museum Burkart, Judith; University of Zurich, Anthropological Institute and Museum Damerius, Laura; University of Zurich, Anthropological Institute and Museum Forss, Sofia; University of Zurich, Anthropological Institute and Museum Koops, Kathelijne; University of Zurich, Anthropological Institute and Museum van Noordwijk, Maria; University of Zurich, Anthropological Institute and Museum Schuppli, Caroline; University of Zurich, Anthropological Institute and Museum
Issue Code: Click here to find the code for your issue.:	INNOVATION
Subject:	Behaviour < BIOLOGY, Evolution < BIOLOGY, Ecology < BIOLOGY
Keywords:	novelty, exploration, learned skills, curiosity, social learning

The reluctant innovator: orang-utans and the phylogeny of creativity

C.P. van Schaik
J. Burkart
L. Damerius
S. I. F. Forss
K. Koops
M. A. van Noordwijk
C. Schuppli

Anthropological Institute & Museum, University of Zurich, Switzerland

Abstract

Young orang-utans are highly neophobic, avoid independent exploration, and show a preference for social learning. Accordingly, they acquire virtually all their learned skills through exploration that is socially induced. Adult exploration rates are also low. Comparisons strongly suggest that major innovations, i.e. behaviours that have originally been brought into the population through individual invention, are made where ecological opportunities to do so are propitious. Most populations nonetheless have large innovation repertoires, because innovations, once made, are retained well through social transmission. Wild orang-utans are therefore not innovative. In striking contrast, zoo-living orang-utans actively seek novelty and are highly exploratory and innovative, probably because of positive reinforcement, active encouragement by human role models, increased sociality, and an expectation of safety. The explanation for this contrast most relevant to hominin evolution is that captive apes generally have a highly reduced cognitive load, in particular due to the absence of predation risk, which strongly reduces the costs of exploration. If the orang-utan results generalize to other great apes, this suggests that our ancestors could become more curious once they had achieved near-immunity to predation on the eve of the explosive increase in creativity characterising the Upper Palaeolithic Revolution.

1. Introduction

Modern human societies thrive on creativity, the disposition of individuals to systematically pursue the generation of novel ideas, products, and procedures (1). Crucially, creativity requires no external trigger such as novelty or an imminent problem that has to be solved but corresponds to an intrinsic interest in exploring and innovating. What are the historical origins of this disposition to be creative, which has led to an unprecedented rate of innovation? A convincing answer to this question is not merely of interest to behavioural biologists and comparative psychologists, but may also have direct applications in the modern world.

Traditionally, most interest in this question has come from palaeo-anthropologists (2). However, because the roots of creativity may precede the hominin lineage, the increasing interest of behavioural biologists (3, 4) and primatologists (5, 6) in animal innovation may help to complete the picture of the phylogenetic origins of human creativity. Because creativity is only one of the diverse processes that can lead to successful innovations, it is useful to examine the various circumstances under which any specific source of innovation can become prevalent. And because great apes are our closest living relatives, the study of the phylogeny of human innovation may be especially productive in this taxon. Here we report on field and captive studies of orang-utans in light of these questions.

Innovation (as a behaviour pattern) refers to a solution to a novel problem, or a new solution to an old problem (7), or, more generally, to novel, learned behaviour patterns acquired by an individual (3, 8). If we define innovativeness as an individual's capacity to innovate, innovativeness can be seen as an expression of problem-solving ability or behavioural flexibility or variability in space or time. Comparative studies have shown a correlation between brain size and problem-solving ability in birds (9, 10) and primates (11, 12), as well as between innovativeness or brain size and colonization success (an expression of flexibility) in birds (13), mammals (14) and lizards (15). In birds, the variety of technical innovations, rather than the tendency to add food types to the diet (arguably representing weaker innovations, more likely among dietary or habitat generalists) was correlated with brain size (16). All these findings strongly suggest that larger-brained organisms are better at solving more (or more difficult) problems, and that humans, being far bigger-brained than any of their relatives, are likely to be even more so.

Although these correlations between innovation and problem solving and brain size are suggestive, they do not necessarily imply that innovation or creativity is a major expression of intelligence in nature, let alone that it is its main function. Field workers rarely witness innovations being made and rarely report that animals are truly curious (with rare exceptions: 17). Moreover, there are major differences between wild and captive animals (18, 19), discussed in detail in section 4. The comparative results therefore do not imply that large brain size automatically implies high innovativeness in nature; animals in nature may deploy their intellectual abilities mainly for different purposes.

The aim of this paper is to examine the conditions favouring innovativeness in orang-utans in order to draw conclusions about the human ancestral state. Similar patterns may apply to the other great apes as well, but because much critical information is still missing for them, our inferences for hominins must remain preliminary. Orang-utans are semi-solitary arboreal apes, living on the South-east Asian islands of Sumatra and Borneo. They are relatively and absolutely large-brained (20), are among the best primate problem solvers (12, 21), and have large innovation repertoires, especially in the subsistence and comfort domains (5, 22, 23).

After a brief terminological excursion, we will first describe skill acquisition in wild orang-utans. A developmental approach is essential because innovations are by definition behaviours that do not have a strong genetic basis and thus do not arise reliably during development, but must instead be acquired and may therefore accumulate with age. We have done extensive studies of skill development in wild orang-utans (24). The data yield the paradoxical result that wild orang-utans are novelty averse, rarely engage in independent exploration, and yet have extensive repertoires of learned skills, which qualify as innovations, which they acquire mostly through socially induced exploration. Wild orang-utans, then, appear to avoid novelty and rarely explore. We then turn to the results of work on orang-utans in zoos and rescue centres and find a striking contrast in novelty response and innovativeness. This so-called captivity effect or captivity bias (19) is also found in other primates, in particular great apes, and allows us to develop a hypothesis for the conditions that make an otherwise exploration-avoidant great ape into a highly exploratory, and thus innovative and even creative one. Finally, we apply this insight to hominin evolution.

2. Innovation and its sources

Innovations are novel, learned behaviour patterns acquired by an individual (3, 8). They are not part of the innate repertoire, nor are they predictably triggered by suitable environmental or social conditions. They therefore do not arise reliably in all maturing individuals of a population, but are instead invented only by a (generally small) subset of all the individuals exposed to the set of conditions in which it can arise.

The most obvious way to recognize innovations is to observe their origin, i.e. when an individual comes up with a behaviour that at that time is new for the population. Each particular innovation has a certain probability of appearing anew in suitable conditions in a given species. This probability can in principle be estimated through experiments (25, 26). Unfortunately, this procedure is rarely feasible, leading most researchers to operationalize the concept by resorting to opportunistic population-level criteria for innovation. The most commonly used measure is that it is novel for the population (3). This operationalization has been very fruitful, but inevitably also introduced some ambiguity in measurement and interpretation. First, the criterion is necessarily imprecise since it obviously depends on the size of the population and the duration of study, and also assumes continuous observation. Fortunately, taking research effort into account makes this measure more reliable, as evident in the persistently obtained correlations with brain size or colonization success mentioned above. Second, this operationalization may have produced a focus on novelty-induced innovations, since they may be most common nowadays, as a result of anthropogenic disturbance. Despite these ambiguities, comparative studies have still yielded clear-cut results, as we saw above, probably because studies tend to rely on similar criteria for rarity (3), and novelty-induced innovations may be a good measure of overall behavioural flexibility.

Confusion has arisen because individuals may also acquire innovations, as defined above, using social learning. Social learning of innovations generally leads to a much higher probability of acquisition than independent exploration does; this probability increases as the mechanisms of social learning deployed become more precise. While relying on social learning, individuals can therefore accumulate a large innovation repertoire without ever making an innovation themselves. The great capacity for social learning in great apes (27) makes this a particularly common pathway of acquisition in this lineage, especially in light of their known cultural repertoires, which are made up of innovations. Orang-utans are an example: they are good social learners (28) and have large cultural repertoires (29). Indeed, in principle, an individual could acquire a large repertoire of innovations without ever making a single innovation.

This approach has given rise to alternative ways of estimating a species' innovation potential. First, one can examine a population's repertoire of innovations using techniques similar to those developed for the recognition of cultural variation (5, 8). Innovations should be rare and will therefore often vary among populations that are otherwise comparable in their environmental conditions and genetic background. A second way is to focus on acquisition. If innovations are acquired through social learning, we must see indications: selective attention and/or socially induced practice (30, 31). Thus, innovations can also be seen as 'learned skills,' as opposed to routine skills that develop reliably in all individuals of the taxon without extensive social learning (Schuppli et al., in prep.). The set of learned skills is broader than the set of innovations as traditionally defined, but as we noted above, innovations are not qualitatively distinct from other behaviours (since there is continuous variation in the probability of independent appearance) and almost certainly not represented as qualitatively different by the individuals in the process of acquiring their behavioural repertoire during development. Nonetheless, it is clear that it is only possible to compare studies that use similar methods to estimate the innovation repertoire of a given species or population.

Perhaps because of the emphasis on novelty-induced innovations, and because the low probability of catching the process of innovation in the act experimentally, the sources of independent innovation in nature, the focus of this paper, are relatively poorly known. Whilst there has been some interest in the cognitive processes underlying innovation (6, 32, 33), there is remarkably little information on what might be called the natural history of innovation: the contexts in which innovations arise in nature. Here we offer a preliminary classification of these contexts. We can use it to identify the main contexts used by orang-utans, and more generally to demarcate creativity relative to the other triggering conditions (Table 1).

Firstly, innovation may arise in response to novelty (some novel element in the environment: object, food item, context, organism, etc.), which usually involves some subsequent exploration (but note that novelty response and exploration are distinctly regulated motivations with distinct functions: 34). Although this pathway has been the focus of much attention, it may actually be rather rare in long-lived and big-brained species where young individuals, who potentially encounter much novelty, avoid it, and by the time they are adult may no longer encounter much that is novel to them (see also below, section 3), unless they engage in long-distance dispersal. Moreover, innovations that tend to arise in this way, such as incorporating novel foods in the diet, are often cognitively simple, and may reflect dietary generalism rather than innovative ability per se (16). Thus, innovative responses to novelty may not be the most important source of innovations in species most comparable to hominins.

Secondly, exploration may be elicited by the failure of pre-existing routines, which requires individuals to find new solutions to old problems and thus lead to innovation, as emphasised by the definition of Kummer & Goodall (7). Thus, a particular technique may no longer work, e.g. because the substrate has changed or the right raw materials are no longer available for tools, and a new way is sought to solve the same problem. This paradigm has most commonly been used experimentally to assess individual innovativeness (35) or to ask whether individuals show cumulative innovations or ratcheting (36, 37). Arguably, failures of pre-existing routines have historically been rare for most species in natural conditions, although they often have increased recently due to anthropogenic disturbance (38, 39). However, they may have become more common at one stage among our ancestors. Potts (40) links the origin of new hominin species and technological innovations to periods of high climate variability.

Thirdly, innovations may simply happen by accident, as a result of the individual going through a routine activity that somehow goes wrong and produces a novel result. For this to happen, the individual must be able to recognize the result as worth retaining and remember the actions that lead to it. It can therefore arise in the absence of exploration. This is a well-known pathway in hominins. Many of the innovations requiring fire, such as heat treatment of stone tools, ceramics or metallurgy, must have been discovered accidentally when the raw materials were exposed to a regular fire (41). It is unclear to what extent such accidents are a major context of innovation in non-humans.

Fourthly, innovation may arise as a result of exploration that was triggered because a clearly defined problem presented itself. For instance, an ape sees a bees' nest and is attracted to the smell, or has learned from previous experience (e.g. because it encountered pieces of honey comb) that this resource is attractive. This well-defined problem elicits targeted exploration, which may occasionally lead to innovation, for instance the use of tools to perforate the nest and extract the honey. Such situations are potentially common, especially in the context of subsistence. Some forms of tool use may have arisen this way (42).

A fifth possibility is that a general lack of access to essential resources (food, shelter, water, mates) may lead to systematic exploration in search of these resources. Systematic exploration may be required because no targeted search is possible given that it is not clear which environmental problems can be solved. This pathway to innovation is captured in the adage "necessity is the mother of invention". Whether this is regarded as creative depends on the weight attached to the spontaneous motivation of the exploration process. Possible instances include innovations made by low-ranking or juvenile individuals that cannot gain access to preferred resources (43-45) or by animals during times of food scarcity (46, 47). There is no evidence for this in orang-utans (42, 48), nor in chimpanzees and bearded capuchin monkeys (42), although others have suggested it is important among chimpanzees and capuchin monkeys (46, 47). In the case of orang-utans, populations with more bark feeding (which happens in response to food scarcity) have smaller innovation repertoires (49). Thus, just because particular innovations would strongly improve fitness does not mean they are therefore made.

Finally, systematic exploration in the absence of obvious eliciting stimuli suggests some level of genuine curiosity: deliberate, intentional searching for a new behaviour pattern, in the absence of any recognised problem or general scarcity. Such intrinsically generated systematic exploration can be playful and spontaneous. Any innovations that arise in this way can be ascribed to creativity. Although creativity is always accompanied by exploration, in the case of humans this may be brief, as most of the creative process takes place in mental simulation. Although modern humans sometimes show this, its importance in human history is contested (50). Moreover, in non-verbal species it may be difficult to demonstrate that systematic exploration is not triggered by some need.

Overall, then, we expect accidental innovations and those that arise in response to a newly recognized problem (entries III and IV in Table 1) to be the most common pathways to innovation among large-brained, long-lived organisms such as great apes.

3. How wild orang-utans acquire their innovations

A young, naïve orang-utan, for whom the whole world is new, continuously encounters novel items. Although this could in principle lead to high rates of independent exploration of unfamiliar items, this is not the case. Field observations on orang-utans have long suggested that they avoid novelty. We therefore decided to test this impression experimentally in our well-habituated study populations at Suaq Balimbing (Sumatra) and Tuanan (Borneo), both inhabiting swamp forests. Small platforms in the shape of ape nests were hoisted into the canopy within the height range of orang-utan travel and provided with novel items, including novel foods. The results (51) showed that wild orang-utans, both Sumatran and Bornean, pass the novel stimulus at a safe distance and avoid approaching novelty for several months (Figure 1.a). In both the Sumatran and the Bornean site only a single (adolescent) individual was ever recorded as contacting the novel items, despite their being available for nearly 5 and over 8 months, respectively.

Instead of individual exploration, orang-utan infants take all their cues from their mother, especially during their first few years of life. Peering at close range at the mother's activities results in interest and subsequent practice (31). Begging plays the same role in food selection (52). Exploration during the pre-weaning years is therefore predominantly targeted at the resources already exploited by the mother. Accordingly, infants largely 'inherit' their mother's diet, even if different females in the same area eat different diets (31), and populations in the same habitat on opposite sides of an impassable river show marked differences in their non-fruit diets (23). After weaning, when maturing individuals begin to range more independently, they still often associate with others and learn from them when they can, but there is also some level of independent exploration. By the time individuals reach adulthood, this has reached extremely low levels of around 1 event per day or less, and in effect only occurs when they are in association (Figure 2; based on Schuppli et al. in prep.). Especially in Borneo, this means exploration has virtually ceased. Moreover, most of the remaining independent exploration can be seen as variation on a theme, where the theme was set by experience, which in turn arose largely as a result of socially induced exploration and skill acquisition. Wild orang-utans therefore show very little evidence of curiosity, except, as noted above, when cued by social information.

These results help us to evaluate the pathways suggested in table 1 for the case of orang-utans. They strongly avoid novelty, eliminating context I. We have not found any examples of context II, which we expected to be rare. The overall scarcity of exploration is consistent with the idea that innovations are rarely induced by necessity (context V), as also suggested by earlier comparisons reviewed above. This may appear surprising but when it comes to food resources, it is not unexpected. During times of great scarcity, orang-utans are in energy-saving mode. They minimize movement and focus on fall-back foods (53). The rarity of spontaneous exploration also argues against context VI, true curiosity.

Additional comparisons among orang-utans, chimpanzees and capuchins (42) strongly suggest that feeding innovations often concern the most nutritious and thus most favoured food sources. In fact, most of the cognitively more demanding feeding innovations mainly concern high-quality foods (39, 42), with few exceptions (46), thus suggesting that opportunistically encountered, clearly defined problem situations triggered innovations (as per context IV in Table 1). Moreover, their presence is predicted by a null-model that links the specific innovation to the opportunities for it to happen, based on the frequency of encounters between the animal and the appropriate context (42).

Along with the near-absence of exploration, these correlations suggest that the majority of innovations arise accidentally or opportunistically (contexts III and IV in Table 1), at least when it comes to subsistence. For now, this conclusion must remain based on plausibility, since it is difficult to conduct the relevant experiments: examining exploration and innovation rates by individuals facing extreme scarcity or finding themselves in novel habitats (or both).

4. Orang-utans in zoos and rescue centres

The same study that examined responses to novelty in wild orang-utans was repeated with zoo animals using the same and very similar sets of novel items (51). The contrast was striking (Figure 1.b). Zoo orang-utans approached novel objects with the same latency as familiar ones, i.e. within seconds rather than months. Thus, zoo orang-utans showed no neophobia.

In other work, we attempted to use the same criteria for innovations as used in the work on wild orang-utans (5). Lehner et al. (54) found that zoo orang-utans have far larger innovation repertoires in comparison with their wild counterparts, even though they had far fewer generations to assemble it. Rehabilitant orang-utans (ex-captives that are being cared for by humans in the enriched conditions of rescue centres and are often trained for release into the wild) are very similar to zoo orang-utans in their response to humans and their general lack of neophobia (L. Damerius, unpubl.). Indeed, the innovation repertoires of rehabilitants when in natural habitats significantly exceed those of wild populations with comparable intensity of observations (Figure 3, taken from data tabulated in ref. 22).

The large size of these innovation repertoires strongly suggests unusual innovation rates amongst zoo and rehabilitant orang-utans. Zoo orang-utans, when provided with the conditions in which orang-utans in some wild populations show particular innovations, not only tended to independently reinvent these same innovations, but also quickly produced several additional variants not seen in nature (54). Similarly, in a study of water use by rehabilitant orang-utans kept on an island in a river, Russon et al. (6) found that they produced various innovations that have never been seen in the wild and are highly unusual for a species that normally avoids deep and flowing water. These results suggest that this difference is not merely due to reduced neophobia among the captive orang-utans, but also to more thorough exploration of the kind akin to curiosity-driven creativity (context VI in Table 1).

It is important to assess whether the orang-utan pattern also holds for other primate species, in particular other great apes. Do they also show high levels of neophobia and low levels of independent exploration in the wild, but show much less neophobia and more exploration in captivity? If so, one can reasonably assume that our hominin ancestors showed similar predispositions too.

A generally more neophobic response to novel foods and novel objects in the wild compared to captivity is not restricted to orang-utans, but has been reported for many nonhuman primates (55, 56), a finding recently replicated for spotted hyaenas (57). In fact, the only species systematically benefiting from approaching novel items may be vagrant species (which therefore often encounter novel situations and items) lacking opportunities to acquire social information, or species living in risk-free habitats. Keas (*Nestor notabilis*), for instance, are parrots living in high mountains in New Zealand in a predator-free habitat. They show true neophilia (17).

Wild chimpanzees are conservative and unwilling to taste novel foods (58), but many readily accept novel food in captivity (59), as in orang-utans. When presented with novel food items, captive chimpanzees were even more hesitant compared to gorillas and orang-utans, and more frequently observed their conspecifics handling the novel items (60). Captive chimpanzee infants are neophobic toward novel foods and pay attention to their mothers before ingesting it (61), suggesting the same pattern in the wild.

Less information is available for exploration than novelty response, and whether captive individuals engage more in independent exploration compared to their wild counterparts, as has been shown for the orang-utans (51). However, the contrast between wild and captive individuals reported for orang-utans holds for several species with regard to innovations. Reader & Laland (62) noted that innovations are relatively more common among zoo-living primates compared to the wild. Many primate species can learn to use or even make tools in captivity that would never do anything like it in the wild (63), and this effect may be found in non-primate species too (19, 64). Captive individuals are better problem solvers in many species of mammals (57, 65, 66) and birds (64, 67).

5. Explaining the contrast

The unexpectedly large contrast between wild and captive orang-utans, and presumably other great apes as well, could reflect increased response to novelty, increased exploration, more effective exploration, or some combination thereof. We will discuss variation in novelty response and exploration, and also compare the results reviewed above with those found in other species.

(a) Novelty response

Given the risk of responding to novelty, individuals should generally benefit from avoiding it, provided they can acquire the relevant information otherwise. Thus, for species and individuals with access to reliable social information it is adaptive to be neophobic (in the functional sense of the term). Indeed, species with long life expectancy, for which the risk of injury or even death are weighted more seriously, should with rare exceptions routinely rely on social information. The data on orang-utans fit this prediction, but so does work on other primates. First, observations on infants closely following adults and paying special attention to adults' activities are reported for many primate species in the wild, from lemurs (68) to macaques (69) to chimpanzees (70). Similar observations are reported for other mammals (71) and birds (72, 73), as well as for captive primates (74). Second, experiments show that naïve individuals lose their neophobia when accompanied or provisioned by others, who may or may not be more knowledgeable (75-77), a finding replicated among orang-utans (61, 78).

The widespread preference for social information suggests that the role of novelty response in producing innovations may well have been overestimated (79). If individuals can rely on social information when immature, they do not need to respond to novelty. Thus, novelty response is unlikely to have been a major source of innovation amongst many non-human primates (4, 33, 51, 80).

In captive orang-utans novelty response may well be a major source of innovation, showing that it can be elicited under the right circumstances. The reduction in neophobia seen in zoo-living orang-utans is best explained by the presence of human keepers that act as trusted role models in the same way that parents or other conspecific caretakers do in nature (51). In effect, then, the captive animals are still relying on social information. In addition, the absence of any negative reinforcement of responses to novelty of all kinds in zoo settings no doubt also contributes to the erosion of neophobic tendencies.

Nonetheless, novelty response alone is unlikely to explain the observed captivity effect, because of the major differences in how and how much animals explore, discussed next.

(b) Exploration tendency

Our data suggest that wild orang-utans are loath to explore. This can be explained by the costs it entails. Firstly, it may entail immediate risks, as when potentially poisonous or dangerous prey or substrates are explored. Secondly, exploration, especially when ultimately unsuccessful due to limited cognitive abilities, entails an opportunity cost, in that it can waste time and energy. Thirdly, and presumably most importantly, the attention devoted to exploration may compete with other vital activities, such as attention to predators or hostile conspecifics (81, 82).

We can therefore develop predictions based on variation in the external (ecological) and internal (life history, niche, age, etc.) factors affecting this trade-off between predation risk and exploration, based on earlier work on the deployment of exploration (62) and social learning (83). However, in many cases, it will be difficult to disentangle the effects of novelty response from those of exploration, because studies of exploration inevitably tend to involve at least some novel elements. The predictions that can be made end up being quite similar to those for novelty response. In general, animals should avoid exploration if they can, unless they cannot afford to because they lack vital skills or resources or unless the risk is so low that it is outweighed by the benefits of learning. Social information should be sought whenever possible, because relying on it is faster and more efficient.

The negligible rate of independent exploration amongst wild orang-utans fits these predictions. The larger innovation repertoires and more complex innovations generally seen among orang-utans living in zoos or rescue centres suggests greatly increased exploration relative to the wild. Zoo-living orang-utans are well-known problem-solvers, including extensive use of tools (84), and can be coaxed into producing innovations that go well beyond the range observed in the wild (37). Likewise, Russon (85, 86) describes the persistence and patience with which recently reintroduced, ex-rehabilitant orang-utans in Borneo try to establish effective feeding techniques.

c) Captivity effect

Various explanations have been offered for the captivity effect (7, 19, 57, 65). One hypothesis emphasizes that humans may act as role models for the animals in captivity (22, 51). Another stresses that animals in captivity have more leisure time due to the absence of predators and because they don't have to forage for their needs (87). We interpret this 'free-time' hypothesis to imply that captivity provides individuals the opportunity to give a task undivided attention for a prolonged period of time, both for independent exploration as well as for exploration triggered by human role models. In nature animals have a higher cognitive load: they are continuously distracted by various tasks that need to be attended to and coordinated as well as plans that need monitoring. Among these tasks, predator vigilance is perhaps most important in many species. Because attention is a limited resource, vigilance interferes with the animals' ability to give a particular task their prolonged, undivided attention (57, 65, 82).

Each species therefore should have an optimum time allocation to exploration, which will largely depend on its safety level. Species living at lower risk of predation should therefore be able to solve more problems or solve the same problem faster than species with lower levels of safety and thus higher levels of necessary vigilance. Thus, all other things being equal, we may expect relatively more prolonged exploration, and thus innovation, in larger rather than smaller species, in arboreal rather than terrestrial species, or species with large groups rather than living solitarily, and in species with sentinels rather than those lacking them. Although these predictions have not yet been tested systematically, some observations support them. For instance, keas do not just lack neophobia, they are also extremely exploratory (17), whereas a comparative study on over 60 parrot species revealed, amongst other results, that parrots on islands are generally less neophobic than their mainland counterparts (88).

Obviously, brain size should be linked to attention span as well: it does not pay to evolve extensive problem-solving abilities if these can never be used. Even if a species relies nearly exclusively on social learning to acquire its skills, this still requires reasoning capacities and prolonged undivided attention because social learning involves many of the same basic cognitive abilities as asocial learning does (89, 90).

6. How about our ancestors?

It has often been noted (e.g. 91) that the rate of change in human technology was remarkably slow, at least when assessed based on the visible parts of the palaeo-archaeological record (i.e. stone artefacts). This strongly suggests that for a long time hominins were very similar to great apes, although at some point in pre-history the rate of change picked up markedly. It also suggests that the ape strategy may also still be common in humans. Indeed, the default strategy of learning by human children remains copying if it is available, even if it is unreliable (92). The same conclusion follows from a tournament organized by Rendell et al. (93), in which the aim was to acquire as much adaptive behaviour as possible in a complex environment. The most successful strategies focussed quite heavily on social learning, and only switched to independent exploration when they could observe no useful innovations from others. The tournament was competitive, and social learning was only possible because agents inadvertently demonstrated the most effective techniques. Thus, if teaching would be added, there would even be less incentive to engage in costly independent exploration.

Routine reliance on copying and avoidance of independent exploration (unless socially induced) may therefore have been the basic ancestral state in humans as well (50). As with apes, then, the default human state is a preference for social learning. Innovations can nonetheless accumulate in a population over time because of the combination of various other pathways to innovation (Table 1) and effective social transmission, especially when teaching is involved.

The number of innovations, in terms of both complexity and diversity of artefacts, gradually increased, but especially during the Upper Palaeolithic Revolution and even more clearly since the Neolithic (94). One explanation for this increase is that it was merely an effect of increased population size. Thus, even if innovations continue to be produced by processes other than creativity, larger populations will show more and more complex innovations, which may create a positive feedback loop without any systematic exploration (50, 95). However, an alternative, or non-exclusive additional, possibility is that the reluctant explorer was turned into a curious and creative explorer under particularly safe conditions (Table 1: necessity-induced [V] or creative [VI]).

The striking captivity effect in orang-utans and other primates may help to explain whether the explosion in cultural complexity was due to creativity or more passive processes. The disappearance of neophobia and the strong increase in exploration among captive orang-utans allows creativity to blossom. This shift is analogous to becoming a top predator, which frees up the mind to explore. This may have happened gradually. Some technological innovation, such as the appearance of stone-tipped weapons or spear-throwers on the eve of the Upper Palaeolithic (96, 97), may finally have turned our ancestors into the top predators in their ecological communities, and so made them virtually immune to predation. The timing of this change corresponds to a major leap in the complexity and diversity of technology known as the Upper Palaeolithic Revolution. Even if it was more gradual than previously assumed (98), there was still a remarkable increase in the rate of cultural change, which has never slowed down since.

This scenario of reduced predation risk as the engine of creativity is plausible. For instance, when people experience the so-called flow and are at their most creative, they are totally oblivious to distractions in the environment (1). Thus, these flow experiences are only possible when not under high predation pressure or other distracting concerns. However, although absence of predation risk is a necessary condition for such concentrated creativity, it is not enough without there being clear incentives for the curious individuals to engage in systematic exploration. Individuals may have begun benefitting from trade based on the appearance of specialization, which in turn is linked to the number and complexity of learned skills needed in daily life. Alternatively, it is possible that at some stage, due to the establishment of cooperative breeding (99), joint innovation became favoured (100).

Regardless of when exactly human creativity began to flourish, it seems safe to conclude that the virtual absence of creativity in wild orang-utans and many other species indicates that our ancestors were not creative until relatively recently. In fact, the results provide some support for the alternative view that until quite recently the feedback between constant rates of accidental innovation and demography provides a plausible alternative to enhanced creativity for changes in human cultural complexity.

Table 1.
The natural history of innovation in large-brained and long-lived species such as great apes: contexts in which novel behaviour patterns may arise.

No.	*Eliciting factor*	*Mechanism*
I- novelty-induced	Novelty	Little or no exploration needed; hence, can only explain simple innovations
II- failure-induced	Failure of specific pre-existing routine induces persistent exploration	Individuals are required to find new solution to old problem, which induces persistent targeted exploration of well-defined problem space
III-accidental	Routine behaviour accidentally leads to innovation	Routine behaviour in absence of novelty, concrete problem or exploration; merely requires recognizing the innovation and remembering the procedures
IV-problem-recognition	Recognizing a novel problem, e.g. the presence of familiar but inaccessible food items	Recognition of the problem and goal-directed exploration and solving of a well-defined problem
V- necessity-induced	Systematic exploration driven by general need (absence of food, shelter, etc)	Extrinsically motivated exploration and innovation of undefined problem space
VI- creative	Systematic exploration in absence of specific problem or novelty	Intrinsically motivated exploration and innovation (curiosity), perhaps playful.

Figure Legends

Figure 1.

Mean latency to first contact by individuals in novel object tests on wild Sumatran (Suaq) and Bornean (Tuanan) orang-utans (a), and Sumatran orang-utans living in zoos in Zurich and Frankfurt (b). Note the logarithmic scale. Note that in each of the wild populations only a single individual ever made contact with the novel objects until the end of the study several months later, whereas the latencies in the zoos refer to means. Thus, the true difference is even greater than suggested by the figure. After Forss et al. (2015).

Figure 2.

Rates of exploration per hour in individual orang-utans of different ages at Suaq Balimbing, Sumatra. Exploration differentiates between socially induced (closed symbols) and spontaneous exploration (open symbols). Note that infant exploration is always socially induced. Definitions follow Jaeggi et al. (2010). After data collected by C. Schuppli (in prep.).

Figure 3.

Innovation repertoires of 4 wild populations of orang-utans compared to those of 4 rehabilitant or recently introduced populations. The data are taken from Russon et al. (2009). Notice that the wild populations had many generations to produce the repertoires whereas the ex-captives had only one or at most two, because most individuals were caught as young infants who had virtually no learned skills.

References

1. Sawyer RK. Explaining Creativity: The science of human innovation. Oxford: Oxford University Press; 2011.
2. Hovers E. Invention, reinvention, and innovation: the makings of Oldowan lithic technology. Developments in Quaternary Science. 2012;16:51-68.
3. Reader SM, Laland KN, editors. Animal Innovation. New York: Oxford University Press; 2003.
4. Brosnan SF, Hopper LM. Psychological limits on animal innovation. Animal Behaviour. 2014;92:325-32.
5. van Schaik CP, van Noordwijk MA, Wich SA. Innovation in wild Bornean orangutans (*Pongo pygmaeus wurmbii*). Behaviour. 2006;143:839-76.
6. Russon AE, Kuncoro P, Ferisa A, Handayani DP. How orangutans (*Pongo pygmaeus*) innovate for water. Journal of Comparative Psychology. 2010;124:14-28.
7. Kummer H, Goodall J. Conditions of innovative behaviour in primates. Philosophical Transactions of the Royal Society, London, series B. 1985;308:203-14.
8. Ramsey G, Bastian ML, van Schaik CP. Animal innovation defined and operationalized. Behavioral and Brain Sciences. 2007;30:393-437.
9. Lefebvre L, Reader SM, Sol D. Brains, innovations and evolution in birds and primates. Brain, Behavior and Evolution. 2004;63:233-46.
10. Overington SE, Morand-Ferron J, Boogert NJ, Lefebvre L. Technical innovations drive the relationship between innovativeness and residual brain size in birds. Animal Behaviour. 2009;78:1001-10.
11. Deaner RO, Isler K, Burkart JM, van Schaik CP. Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. Brain, Behavior and Evolution. 2007;70(2):115-24.
12. Reader SM, Hager Y, Laland KN. The evolution of primate general intelligence. Philosophical Transactions of the Royal Society of London. 2011;366:1017-27.
13. Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L. Big brains, enhanced cognition, and response of birds to novel environments. Proceedings National Academy of Sciences USA. 2005;102:5460–5.
14. Sol D, Bacher S, Reader SM, Lefebvre L. Brain size predicts the success of mammal species introduced into novel environments. American Naturalist. 2008;172:S63-S71.
15. Amiel JJ, Tingley R, Shine R. Smart moves: effects of relative brain size on establishment success of invasive amphibians and reptiles. PLoS One. 2011;6(4):e18277.
16. Ducatez S, Clavel J, Lefebvre L. Ecological generalism and behavioural innovation in birds: technical intelligence or the simple incorporation of new foods? Journal of Animal Ecology. 2015;84:79-89.
17. Huber L, Gajdon GK. Technical intelligence in animals: the kea model. Animal Cognition. 2006;9:295-305.
18. van Schaik CP, Deaner RO, Merrill MY. The conditions for tool use in primates: implications for the evolution of material culture. Journal of Human Evolution. 1999;36:719-41.
19. Haslam M. 'Captivity bias' in animal tool use and its implications for the evolution of hominin technology. Philosophical Transactions of the Royal Society of London. 2013;368:20120421.
20. Dunbar RIM, Shultz S. Evolution in the Social Brain. Science. 2007;317:1344-7.
21. Deaner RO, van Schaik CP, Johnson V. Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. Evolutionary Psychology. 2006;4:149-96.
22. Russon AE, van Schaik CP, Kuncoro P, Ferisa A, Handayani DP, van Noordwijk MA. Innovation and intelligence in orangutans. In: Wich SA, Utami SA, Mitra ST, van Schaik CP, editors. Orangutans Compared: Oxford University Press; 2009. p. 279-98.

23. Bastian ML, Zweifel N, Vogel E, Wich SA, van Schaik CP. Diet traditions in wild orangutans. American Journal of Physical Anthropology. 2010;143:175-87.
24. Schuppli C, Isler K, van Schaik CP. How to explain the unusually late at skill competence among humans? Journal of Human Evolution. 2012;63:843-50.
25. Terkel J. Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). In: Heyes CM, Galef BG, Jr., editors. Social Learning in Animals: The Roots of Cultures. San Diego: Academic Press; 1996. p. 17-48.
26. Morand-Ferron J, Lefebvre L, Reader SM, Sol D, Elvin S. Dunking behaviour in Carib grackles. Animal Behaviour. 2004;68:1267-74.
27. Whiten A. Social learning, traditions, and culture. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB, editors. The Evolution of Primate Societies. Chicago: The University of Chicago Press; 2012. p. 682-700.
28. Russon A, Galdikas B. Imitation in ex-captive orangutans. Journal of Comparative Psychology. 1993;107:147-61.
29. van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, et al. Orangutan cultures and the evolution of material culture. Science. 2003;299:102-5.
30. Lonsdorf EV. What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? Animal Cognition. 2006;9:36-46.
31. Jaeggi AV, Dunkel L, van Noordwijk MA, Wich SA, Sura AAL, van Schaik CP. Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. American Journal of Primatology. 2010;72:62-71.
32. Reader SM. Innovation and social learning: individual variation and brain evolution. Animal Biology. 2003;53:147-58.
33. Griffin AS, Guez D. Innovation and problem solving: A review of common mechanisms. Behavioural Processes. 2014;109:121-34.
34. Mettke-Hoffman C. Cognitive ecology: ecological factors, life-styles, and cognition. WIREs Cognitive Science. 2014;5:345-60.
35. Burkart JM, Foglia M, Strasser A. Trade-offs between social learning and individual innovativeness in common marmosets, *Callithrix jacchus*. Animal Behaviour. 2009;77:12191-1301.
36. Tomasello M, Kruger AC, Ratner HH. Cultural learning. *Behavioral and Brain Sciences*. 1993;16:495-552.
37. Lehner SR, Burkart JM, van Schaik CP. Can captive orangutans (*Pongo pygmaeus abelii*) be coaxed into cumulative build-up of techniques? Journal of Comparative Psychology. 2011;125:446-55.
38. van Schaik CP. Fragility of traditions: The disturbance hypothesis for the loss of local traditions in orangutans. International Journal of Primatology. 2002;23:527-38.
39. Sanz CM, Morgan DB. The social context of chimpanzee tool use. In: Sanz CM, Call J, Boesch C, editors. Tool Use in Animals: Cognition and Ecology. Cambridge, UK: Cambridge University Press; 2013. p. 161-75.
40. Potts R. Environmental and behavioral evidence pertaining to the evolution of early *Homo*. Current Anthropology. 2012;53:S299-S317.
41. van Schaik CP. The Primate Origins of Human Nature. New York: Wiley-Blackwell; 2016.
42. Koops K, Visalberghi E, van Schaik CP. The ecology of primate material culture. Biology Letters. 2014;10:20140508.
43. Laland KN, Reader SM. Foraging innovation is inversely related to competitive ability in male but not female guppies. Behavioral Ecology. 1999;10:270-4.
44. Reader SM, Laland KN. Primate innovation: sex, age and social rank differences. International Journal of Primatology. 2001;22(5):787-805.
45. Thornton A, Samson J. Innovative problem solving in wild meerkats. Animal Behaviour. 2012;83:1459-68.

46. Yamakoshi G. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. American Journal of Physical Anthropology. 1998;106:283-95.

47. Moura ACdA, Lee, P. C. Capuchin tool use in caatinga dry forest. Science. 2004;306:1909.

48. Fox EA, van Schaik CP, Sitompul A, Wright DN. Intra-and interpopulational differences in orangutan (*Pongo pygmaeus*) activity and diet: implications for the invention of tool use. American Journal of Physical Anthropology. 2004;125:162-74.

49. Burkart JM, van Schaik CP. Determinanten innovativen Verhaltens bei nichtmenschlichen Primaten. In: Schmidinger H, Sedmak C, editors. Topologien des Menschlichen. Darmstadt: Wissenschaftliche Buchgesellschaft; 2008. p. 275-98.

50. Henrich J. The evolution of innovation-enhancing institutions. In: O'Brien MJ, Shennan S, editors. Innovation in Cultural Systems: Contributions from evolutionary anthropology. Cambridge, MA: MIT Press; 2010. p. 99-120.

51. Forss SIF, Schuppli C, Haiden D, Zweifel N, van Schaik CP. Contrasting responses to novelty by wild and captive orangutans. American Journal of Primatology. 2015;XXX.

52. Jaeggi AV, van Noordwijk MA, van Schaik CP. Begging for information: Mother-offspring food sharing among wild Bornean orangutans. American Journal of Primatology. 2008;70:533-41.

53. Morrogh-Bernard H, Husson SJ, Knott CD, Wich SA, van Schaik CP, van Noordwijk MA, et al. Orangutan activity budgets and diets. In: Wich SA, Mitra Setia T, Utami Atmoko SA, Van Schaik CP, editors. Orangutans Compared: Geographic Variation in Behavioral Ecology and Conservation. Oxford: Oxford University Press; 2009. p. 119-33.

54. Lehner SR, Burkart JM, van Schaik CP. An evaluation of the geographic method for recognizing innovations in nature, using zoo orangutans. Primates. 2010;51:101-18.

55. Menzel EW, Jr. Responsiveness to objects in free-ranging Japanese monkeys. Behaviour. 1966;26:130-50.

56. Visalberghi E, Janson CH, Agostini I. Response toward novel foods and novel objects in wild *Cebus apella*. International Journal of Primatology. 2003;24:653-75.

57. Benson-Amram S, Weldele ML, Holekamp KE. A comparison of innovative problem-solving abilities between wild and captive spotted hyaenas, *Crocuta crocuta*. Animal Behaviour. 2013;85:349-56.

58. Nishida T, Wrangham RW, Goodall J, Uehara S. Local differences in plant-feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park, Tanzania. Journal of Human Evolution. 1983;12:467-80.

59. Addessi E, Visalberghi E. How social influences affect food neophobia in captive chimpanzees: a comparative approach. In: Matsuzawa T, Tomonaga M, Tanaka M, editors. Cognitive Development in Chimpanzees. Tokyo: Springer; 2006. p. 246-64.

60. Gustafsson E, Saint Jalme M, Bomsel M-C, Krief S. Food neophobia and social learning opportunities in great apes. International Journal of Primatology. 2014;35:1037-71.

61. Ueno A, Matsuzawa T. Food transfer between chimpanzee mothers and their infants. Primates. 2004;45:231-9.

62. Reader SM, Laland KN. Animal innovation: an introduction. In: Reader SM, Laland KN, editors. Animal Innovation. Oxford: Oxford University Press; 2003. p. 3-35.

63. Shumaker RW, Walkup KR, Beck BB. Aniaml Tool Behavior: The Use and Manufacture of Tools by Animals. Baltimore, MD: Johns Hopkins University Press; 2011.

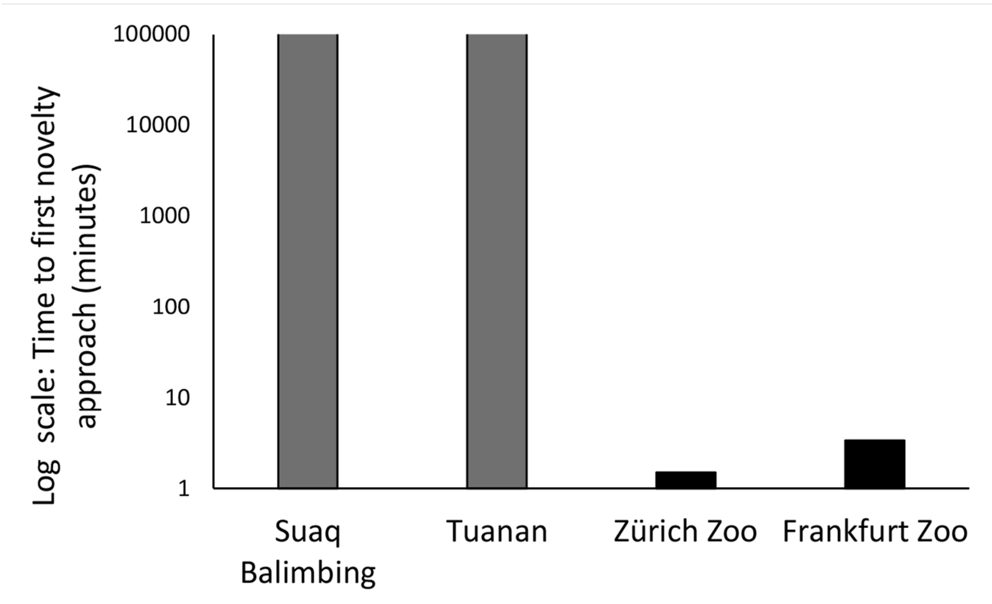
64. Bird CD, Emery NJ. Insightful problem solving and creative tool modification by captive nontool-using rooks. Proceedings National Academy of Sciences USA. 2009;106:10370-5.

65. Halsey LG, Bezerra BM, Souto AS. Can wild common marmosets (*Callithrix jacchus*) solve the parallel strings task? Animal Cognition. 2006;9:229-33.

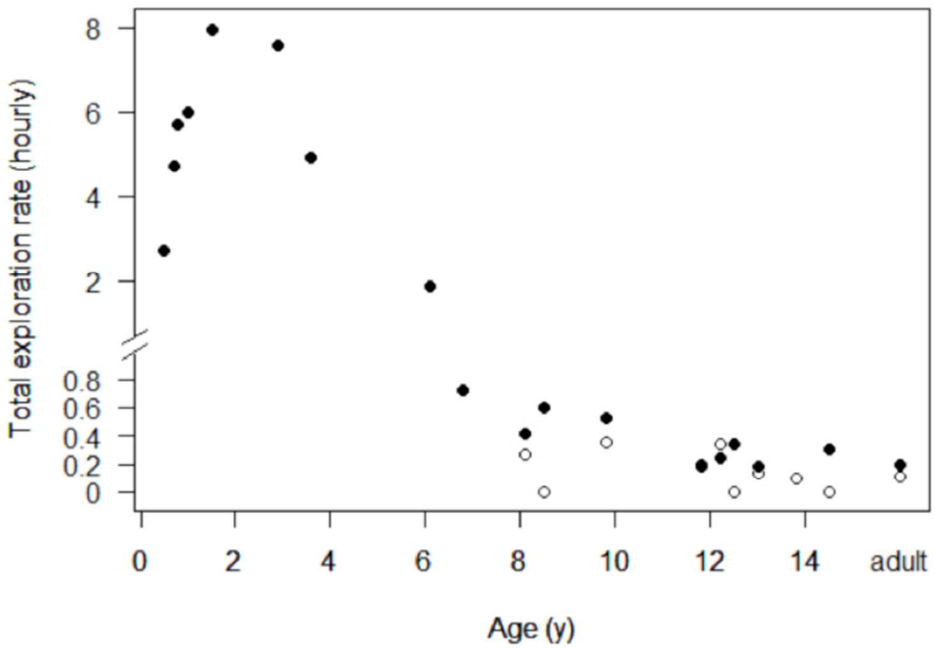
66. Laidre ME. Spontaneous performance of wild babons on three novel food-access puzzles. Animal Cognition. 2008;11:223-30.

67. Gajdon GK, Fijn N, Huber L. Testing social learning in a wild mountain parrot, the kea (*Nestor notabilis*). Learning & Behavior. 2004;32:62-71.
68. Tarnaud L. Ontogeny of feeding behavior of *Eulemur fulvus* in the dry forest of Mayotte. International Journal of Primatology. 2004;25:803-24.
69. Tarnaud L, Yamagiwa J. Age-dependent patterns of intensive observation on elders by free-ranging juvenile Japanese macaques (*Macaca fuscata yakui*) within foraging context on Yakushima. American Journal of Primatology. 2008;70:1103-13.
70. Humle T, Snowdon CT, Matsuzawa T. Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. Animal Cognition. 2009;12:S37-S48.
71. Rymer T, Schradin C, Pillay N. Social transmission of information about novel food in two populations of the African striped mouse, *Rhabdomys pumilio*. Animal Behaviour. 2008;76:1297-304.
72. Chiarati E, Canestrari D, Vera R, Baglione V. Subordinates benefit from exploratory dominants: response to novel food in cooperatively breeding carrion crows. Animal Behaviour. 2012;83:103-9.
73. Stöwe M, Bugnyar T, Heninrich B, Kotrschal K. Effetcs of group size on approach to novel objects in ravens (*Corvus corax*). Ethology. 2006;112:1079-88.
74. Ueno A, Matsuzawa T. Response to novel food in infant chimpanzees. Do infants refer to mothers before ingesting food on their own? Behavioral Processes. 2005;68:85-90.
75. Addessi E, Chiarotti F, Visalberghi E, Anzenberger AA. Response to novel food and the role of social influences in common marmosets (*Callithrix jacchus*) and Goeldi's monkeys (*Callimico goeldii*). American Journal of Primatology. 2007;9999(9999):n/a.
76. Leca JB, Gunst N, Watanabe K, Huffman MA. A new case of fish-eating in japanese macaques: Implications for social constraints on the difusion of feeding innovation. American Journal of Primatology. 2007;69:1-8.
77. Thornton A. Social learning about novel foods in young meerkats. Animal Behaviour. 2008;76:1411-21.
78. Hardus ME, Lameira AR, Wich SA, de Vries H, Wahyudi R, Shumaker RW, et al. Effects of repeated exposures and sociality on novel food acceptance and consumption by orangutans. Primates. 2015;56 21-7.
79. Boesch C. Innovation in wild chimpanzees (Pan troglodytes). Intern J Primatol. 1995;16:1-16.
80. Forss S. Social learning and independent exploration in immature Sumatran orangutans, *Pongo abelii* [Master Thesis]. Zurich, CH: University of Zurich; 2009.
81. Lawrence ES. Vigilance during 'easy' and 'difficult' foraging tasks. Animal Behaviour 33. 1985:1373-5.
82. Dukas R. Evolutionary biology of limited attention. In: Tomassi L, Peterson MA, Nadel.L., editors. Cognitive Biology: Evolutionary and developmental perspectives on mind, brains and behavior. Cambridge, MA: MIT Press; 2009. p. 147-62.
83. Galef BG, Jr., Giraldeau L-A. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim Behav. 2001;61:3-15.
84. Lethmate J. Problemlöseverhalten von Orang-Utans (*Pongo pygmaeus*). Berlin: Verlag Paul Parey; 1977.
85. Russon AE. Return of the native: cognition and site-specific expertise in orangutan rehabilitation. International Journal of Primatology. 2002;23:461-78.
86. Russon AE. Acquisition of complex foraging skills in juvenile and adolescent orangutans (*Pongo pygmaeus*): developmental influences. Aquatic Mammals. 2006;32:500-10.
87. Kummer H. Weisse Affen am Roten Meer. Das soziale Leben der Wüstenpaviane. München: Piper; 1992.
88. Mettke-Hofmann C, Winkler H, Leisler B. The significance of ecological factors for exploration an neophobia in parrots. Ethology. 2002;108:249-72.

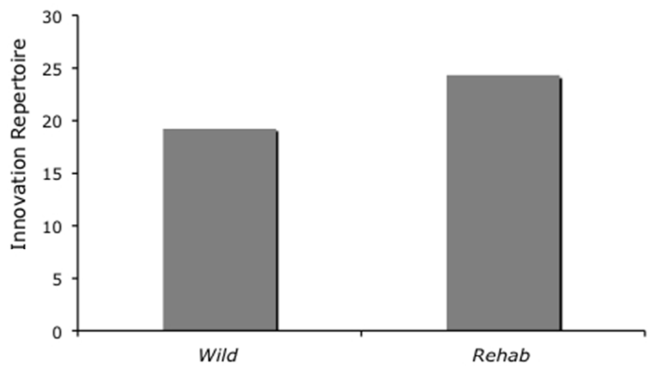
89. van Schaik CP, Burkart JM. Social learning and evolution: the cultural intelligence hypothesis. Philosophical transactions of the Royal Society of London. 2011;366:1008-16.
90. Heyes C. What's social about social learning? Journal of Comparative Psychology. 2012;126:193-202.
91. Durham WH. Coevolution: Genes, Culture, and Human Diversity. Stanford, CA: Stanford University Press; 1991.
92. Carr K, Kendal RL, Flynn EG. Imitate or innovate? Children's innovation is influenced by the efficacy of observed behaviour. Cognition. 2015;142:322-32.
93. Rendell L, Boyd R, Cownden D, Enquist M, Eriksson K, Feldman MW, et al. Why copy others? Insights from the social learning strategies tournament. Science. 2010;328:208-13.
94. Richerson PJ, Boyd R. Not by Genes Alone: How Culture Transformed Human Evolution. Chicago: University of Chicago Press; 2005.
95. Shennan S. Long-term trajectories of social change. In: Richerson PJ, Christiansen MH, editors. Cultural Evolution: Society, Technology, Language, and Religion. Cambridge, MA: MIT Press; 2013. p. xx-yy.
96. Shea JJ. The origins of lithic projectile point technology: evidence from Africa, the Levant, and Europe. Journal of Archaeological Science. 2006;33:823-46.
97. Marlowe FW. Hunter-gatherers and human evolution. Evolutionary Anthropology. 2005;14:54-67.
98. McBrearty S, Brooks AS. The revolution that wasn't: a new interpretation of the origin of modern human behavior. Journal of Human Evolution. 2000;39:453-563.
99. Burkart JM, Hrdy SB, van Schaik CP. Cooperative breeding and human cognitive evolution. Evolutionary Anthropology. 2009;18:175-86.
100. Wilson DS, Timmel JJ, Miller RR. Cognitive cooperation: when the going gets tough, think as a group. Human Nature. 2004;15:225-50.



Mean latency to first contact by individuals in novel object tests on wild Sumatran (Suaq) and Bornean (Tuanan) orang-utans (a), and Sumatran orang-utans living in zoos in Zurich and Frankfurt (b). Note the logarithmic scale. Note that in each of the wild populations only a single individual ever made contact with the novel objects until the end of the study several months later, whereas the latencies in the zoos refer to means. Thus, the true difference is even greater than suggested by the figure. After Forss et al. (2015).
125x76mm (300 x 300 DPI)



Rates of exploration per hour in individual orang-utans of different ages at Suaq Balimbing, Sumatra. Exploration differentiates between socially induced (closed symbols) and spontaneous exploration (open symbols). Note that infant exploration is always socially induced. Definitions follow Jaeggi et al. (2010). After data collected by C. Schuppli (in prep.).
255x182mm (72 x 72 DPI)



Innovation repertoires of 4 wild populations of orang-utans compared to those of 4 rehabilitant or recently introduced populations. The data are taken from Russon et al. (2009). Notice that the wild populations had many generations to produce the repertoires whereas the ex-captives had only one or at most two, because most individuals were caught as young infants who had virtually no learned skills.
254x190mm (72 x 72 DPI)

Table 1.
The natural history of innovation in large-brained and long-lived species such as great apes: contexts in which novel behaviour patterns may arise.

innovation type	***Eliciting factor***	***Mechanism***
I- novelty-induced	Novel object or situation	Often little or no exploration needed; hence, can only explain simple innovations
II- failure-induced	Failure of specific pre-existing routine induces persistent exploration	Individuals are required to find new solution to old problem, which induces persistent targeted exploration of well-defined problem space
III-accidental	Routine behaviour accidentally leads to innovation	Routine behaviour in absence of novelty, concrete problem or exploration; merely requires recognizing the innovation and remembering the procedures
IV-problem-recognition	Recognizing a novel problem, e.g. the presence of familiar but inaccessible food items	Goal-directed exploration and solving of a well-defined problem
V- necessity-induced	General need (absence of food, shelter, etc)	Extrinsically motivated systematic exploration and innovation of undefined problem space
VI- creative	Curiosity in absence of specific problem or novelty	Intrinsically motivated exploration and innovation (curiosity), perhaps playful.